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FACTORS INFLUENCING THE ORIENTATION OF MIGRATING ANADROMOUS FISHES

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FACTORS INFLUENCING THE ORIENTATION OF MIGRATING ANADROMOUS FISHES

By Gerald B. Collins, *Fishery Research Biologist*

HISTORICAL BACKGROUND

The orientation of migrating fishes has been the subject of investigation and conjecture for many years. Migration paths have been outlined by tagging experiments, and a wealth of valuable information on the physiology, development, and behavior of migratory fishes has been acquired through the persistent efforts of many able investigators; but the means by which the fish are directed on their migrations are still largely a matter of speculation.

The purpose of the study presented here was to investigate the influence of certain physical and chemical factors upon the orientation of migrating anadromous fish of the genus *Pomolobus*. In the course of this investigation an effort was made to determine experimentally if the migrating fish would orient to differences in the physical and chemical characteristics of water.

The existence of differences in physical and chemical factors in natural waters to which fish might respond has long been known. Slight gradations usually exist in the relative amounts of dissolved gases, in *p*H, in temperature, and in other physical and chemical characteristics of a stream from the source to the mouth. Such gradients are usually so slight that the differences between points miles apart are still below the thresholds of the sensory perception of fish.

Much greater gradients are found at stream junctions and at stream entrances into lakes or into the sea. In these gradients there frequently are chemical and physical differences between points a few feet apart which are large enough to be detected by the fish. The existence of these gradients at crucial points along the migration paths of anadromous fishes where they might influence the fish in the selection of a stream has led to speculation on their possible role in directing the migration of the fish.

The author is greatly indebted to Prof. George L. Clarke of Harvard University for his encouragement, helpful suggestions, and criticisms during this research. The work was done in partial fulfillment of the requirements for the degree of doctor of philosophy at Harvard University, Department of Biology.

Thanks are due also to Prof. Alfred C. Redfield and many other members of Harvard University and the Woods Hole Oceanographic Institution for their advice and aid in securing funds and special equipment. The research during the summer of 1949 was done while occupying a research fellowship at the Woods Hole Oceanographic Institution.

The cooperation of the town of Bourne, Mass., is acknowledged for permission to work in Herring River and to use town property at Bournedale.

A special debt is gratefully acknowledged to Director Francis W. Sargent and John Burns of the Division of Marine Fisheries, Massachusetts Conservation Department, for their interest and aid which made this investigation possible. The research in the spring of 1949 was done as an employee of the Massachusetts Division of Marine Fisheries.

The encouragement and aid of Dr. Lionel A. Walford, Ralph P. Silliman, Clinton E. Atkinson, and others of the Fish and Wildlife Service are also acknowledged. The research in the spring of 1950 was done as an employee of the U. S. Fish and Wildlife Service.

MAJOR THEORIES ON ORIENTATION

Currently, two major concepts on the orientation of migrating anadromous fishes have gained wide support; and, while not mutually exclusive, they are, as the frequent clashes in the literature suggest, not entirely compatible.

One of these theories regards the upstream migration of the fish as a purposeful "homing" to the part of the river system in which it was hatched or in which it spent the early stages of

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its life. Memory impressions of the goal or home are implied and the fish is said to be seeking its spawning area. The fish is thought to return to its native stream because that was the place where it was spawned rather than because the stream was more accessible or made more attractive by immediate environmental conditions. The fact that significant numbers of fish have actually been observed to return to the streams from which they originated is frequently used as evidence for this homing viewpoint.

The other theory is that environmental factors control the direction of migration, and therefore physical and chemical conditions such as temperature, current, amounts of dissolved gases, or odors, are thought to determine the ultimate destination of the fish. These factors fluctuate and are duplicated in nature so that migratory fish could go to any stream with these conditions.

Those who support the idea of environmental control of the direction of migration present evidence that the fish responds to its immediate environment at each point of its migration and they look upon the migration itself as merely the sum of the successive responses. The various species are thought to arrive at their separate destinations because they respond in specifically different ways to the existing patterns of environmental stimuli. The return of many fish to the stream of their origin is to be expected, according to this viewpoint, because the patterns of environmental conditions which direct them persist year after year.

Variations of these views may be found expressed under different interpretations of the "parent stream" or "home stream" theory developed by investigators working on salmon migration. An excellent review of major problems and controversial questions in salmon migration is afforded by the symposium, "The Migration and Conservation of Salmon," published in 1939 by the American Association for the Advancement of Science.

SENSORY BASIS OF ORIENTATION

Whether the migratory fish has purpose and seeks its native stream or whether the fish is entirely directed by immediate environmental factors along its route, its orientation must be achieved by some sensory means.

With fish migration, as with bird migration, there has been much speculation over the possible existence of a special sensory perception that is unknown at present. No physical basis for this has ever been found nor have such sensory abilities ever been demonstrated. There is evidence that fish can see, hear, taste, and smell. It is known that they can respond to tactile and kinesthetic stimuli, react to acceleration and nonrectilinear motion, and maintain equilibrium. It has been demonstrated that they can respond to temperature and to various chemical substances by means other than taste or smell. In the absence of any evidence to the contrary, it is reasonable to suppose that these sensory abilities are the ones by which fish are guided while on their migrations. Therefore, it appears logical to explore fully the relation between these known sensory abilities and prevailing environmental patterns before considering hypothetical sensory abilities.

RELATION OF SENSORY ABILITIES TO ENVIRONMENTAL PATTERNS

As the sensory abilities of fishes have been revealed and delineated many investigations have been made to examine their relation to migration. Chidester (1924)[1] pointed out the number and diversity of these investigations as well as their apparently contradictory evidence.

Attention was turned to natural environmental patterns which might have a directional influence upon fish with the known sensory abilities. The physical and chemical gradients which exist along the migration paths of anadromous fishes were examined for their possible role in orienting migrating fish.

The observations of Ward (1920) in Alaska led him to believe that temperature was an important factor in the choice of a spawning stream by sockeye salmon, *Oncorhynchus nerka*. He observed that on the upstream migration the fish pass from swift to slow water and vice versa, that they go from shallow to deep water and vice versa, and that they move from turbid to clear water and vice versa. However, he found that at the junction of two streams the sockeye salmon consistently chose the colder stream and he concluded that temperature was the chief orienting factor.

[1] For references referred to parenthetically, see Literature Cited, p. 395.

The earlier investigations of Chamberlain (1907) in Alaska also indicated that temperature influenced the selection of streams by sockeye salmon. However, Chamberlain found that the sockeye chose the warmer streams.

Foerster (1929) observed the migration of sockeye salmon near Cultus Lake, British Columbia, and found the sockeye at one time entering the colder stream and at another time selecting a warmer stream. He concluded that temperature probably had very little directing influence on the upstream migration of the sockeye salmon. Foerster also made measurements of the *p*H and of the dissolved oxygen in the streams, but was unable to find any correlation between variations in these factors and the selection of streams by the sockeye salmon.

Roule (1933) expressed the opinion that the direction of shad, *Paralosa nilotica rhodanensis* and *Alosa alosa*, migration was controlled by temperature. He pointed out that the migration begins when the river water, pouring into the sea in estuaries, is at a higher temperature than that of the sea. Roule related that in one section of the Rhone River shad fishermen always set their traps on only one bank of the river, whereas along most of the river they set traps on both banks. Investigation revealed that the water on one side of the river was several degrees warmer than on the other due to the influence of a warm tributary upstream. The shad were always found migrating on the warmer side; and they were also observed to turn off the main stream into certain tributaries which were warmer than the main stream. Roule's observations on the behavior of salmon, *Salmo salar*, during migration convinced him that the salmon were indifferent to temperature.

Roule (1914), observing the selection of particular streams by the Atlantic salmon, *Salmo salar*, in its upstream migration to spawning areas, concluded that the proportion of dissolved O_2 in the water was the dominant factor in directing the migration. He maintained that the salmon always choose the water with a higher concentration of dissolved O_2. Roule (1933) suggested that the metabolic condition of the fish results in increased respiratory activity and it becomes polarized toward the more highly oxygenated water. Roule used the word "branchiotropism" to describe deviations in direction brought about by respiratory influences. He maintained that the "branchiopolarity" of the salmon drives it forward and acts as its guide.

Chevey, Roule, and Verrier (1927) blamed the depletion of salmon runs in certain streams on the lack of dissolved O_2 in the streams owing to mill wastes. Their investigations indicated that salmon would not enter a stream with a low dissolved O_2 content. The observation that the shad, *Alosa alosa*, were not affected by the low O_2 content of the water pointed to a marked species difference.

Russell (1934) did not agree with the findings of Roule and his coworkers. He pointed out that in the mouths of certain salmon rivers, such as the Tees and the Tyne, there is a long stretch of heavily polluted water in which the O_2 content may fall very low. However, salmon enter and ascend these rivers.

Shelford and Powers (1915) using a gradient tank technique, found that herring fry, *Clupea pallasi*, would orient to differences in temperature and dissolved gases. Powers became convinced that gradients of CO_2 tension exert an important influence upon the orientation of migrating fishes. Powers and Hickman (1928) measured the CO_2 tension in lakes, in rivers draining lakes, and in rivers which did not drain lakes in the Fraser and the Columbia River systems. They found that, in general, lakes and rivers draining lakes had a lower CO_2 tension (average 0.57 mm. Hg) than rivers not fed by lakes (average 1.05 mm. Hg). Further analysis of the data also indicated that typical mountain streams had higher CO_2 tensions than streams of the lowland.

Powers (1939) pointed to an observation that the sockeye salmon, given a choice, will always choose the fork of a river which drains a lake. The chinook salmon, *Oncorhynchus tshawytscha*, in the same situation apparently is indifferent and moves up either branch. Powers suggested that the sockeye is responding to differences in CO_2 tension in its selection of a stream draining a lake. The lack of a similar response on the part of the chinook salmon was presumably looked upon as a species difference.

The publications of these investigators who were seeking to correlate the observed movements of migratory fishes to gradients of temperature and of dissolved gases were received with great

interest. There has been, however, a general reluctance on the part of many engaged in fishery research to accept some of the conclusions put forth. Those investigators who were convinced of a highly developed homing ability in anadromous fishes found it difficult to reconcile the idea of migrating fishes responding to environmental gradients with that of homing. Many contradictory observations made by other workers in the field, because of a general tendency to avoid negative reporting, seldom reached the literature. Furthermore, field workers who were aware of the enormous difficulties in making dependable observations of the movements of fish in large rivers and streams, particularly with only intermittent observations made over a wide area, felt that the evidence upon which the conclusions were based was inadequate.

In summarizing previous research in this field it might be said that—

(1) The ability of fishes to detect differences in temperature and in amounts of dissolved gases has been established experimentally.
(2) Laboratory (gradient-tank) experiments have also established that differences in temperature and in amounts of dissolved gases can influence the direction of fish movement.
(3) Differences in water temperature and amounts of dissolved gases have been shown to exist in natural waters at points where they might exert an important influence upon the direction of migrating anadromous fishes.
(4) It has been suggested that these physical and chemical differences do influence the orientation of the migrating fish.
(5) Some field observations of migratory-fish behavior appear to show a relation between the direction of migration and gradients of certain physical and chemical factors. These field observations are relatively few, inconclusive, and contradictory.

Thus, it is known that some fishes can orient with reference to certain physical and chemical differences in water, but whether migrating anadromous fishes actually do orient with reference to such differences is not known. The following experiments were undertaken to explore this question with one type of anadromous fish.

EXPERIMENTAL APPROACH

In studying the influence of gradients of physical and chemical characteristics of water upon the orientation of migrating anadromous fishes a direct experimental approach was used. Experiments were undertaken which attempted to measure the directional responses of migrating fishes of the genus *Pomolobus* to certain differences in water characteristics including temperature, *p*H, and amounts of dissolved gases (O_2, N_2, and CO_2).

The experiments were designed to avoid many complications that have to be considered in laboratory experiments with live fish. The experiments were made in the stream in which the fish were migrating so that the fish would not be handled or subjected to the shock of being removed from their natural environment. Tests were made on thousands of fish, and each fish was tested only once so that considerations involving learning could be ignored.

Inasmuch as the special migratory behavior of anadromous fishes is exhibited for only limited periods of time, perhaps only once or twice during the life of the fish, an essential condition of these experiments was that they were conducted while the fish were actually migrating. The importance of this is realized when one considers how greatly the response of a fish to environmental stimuli may differ at various physiological stages of its life. As fingerlings, the fish are found migrating downstream; as maturing adults, they migrate upstream. In those species which survive spawning, the spent fish again migrate downstream. Frequently, individual fish of the same species may be found in a stream responding in very different ways to identical environmental stimuli.

The differences in physical and chemical factors tested were artificially produced in these experiments but the type and magnitude of the differences were within the range commonly found at stream junctions in nature.

MATERIALS AND METHODS

The experiments were conducted in the Herring River at Bournedale, Mass., in 1949 and 1950 during the spring herring runs. The herring run at Bournedale actually consists of two overlapping runs of closely related species. The earlier run, made up of alewives, *Pomolobus pseudoharengus* (Wilson), begins about the first of April and continues until the end of May. The second and smaller run of glut herring, *Pomolobus aestivalis*

(Mitchill), usually starts about the last week of May and lasts until the middle of June.

There are visible external differences by which these two species can be identified. The glut herring is generally smaller than the alewife, has a smaller eye in relation to the head, and when examined out of water has darker dorsal pigmentation. The individual variations in size within the two groups overlap considerably, and in the water each species has the ability to modify its pigment to blend with the background in the matter of a few seconds. Consequently, it is very difficult to distinguish between the two species with any degree of certainty without first removing the fish from the water. Attempts to separate the two species while the experiments were in progress proved to be impractical. When the studies were completed, a careful comparison of the responses shown by the fish in experiments conducted at the beginning of the early run when only alewives were present with those in experiments made near the end of the later run when only glut herring were present, failed to reveal any differences between the responses of the two species.

These anadromous members of the herring family (Clupeidae) proved to be ideally suited to experimental purposes. They are small and migrate in enormous numbers through easily accessible brooks and streams (fig. 1). The construction of the experimental apparatus and the conditioning of water for experiments with these fishes can be done on a smaller, less expensive scale than would be necessary for fishes such as the shad or the salmon. At Bournedale each year during the herring run, more than half a million of these fishes enter the small Herring River (completely fresh water; average flow less than 20 c. f. s.) from the sea water of the Cape Cod Canal and migrate upstream for approximately a mile to their spawning grounds in Great Herring Pond. The experiments were conducted in the stream a short distance below its entrance into Great Herring Pond.

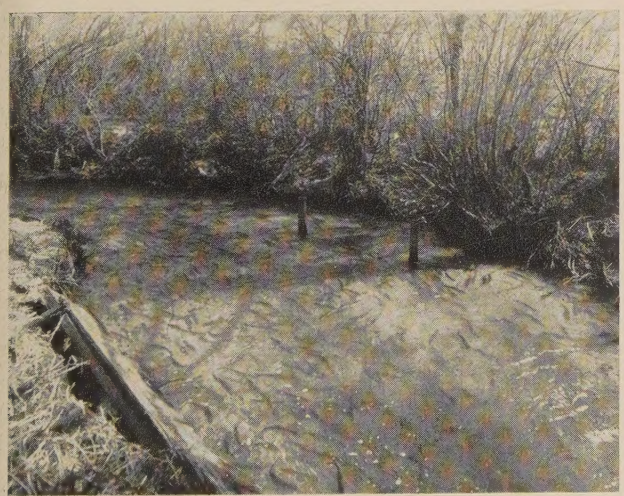

FIGURE 1.—The herring run at Bournedale, Mass. This pool is immediately below the experimental station.

EXPERIMENTAL METHOD

As the fish migrated upstream, they were directed by wire screens into a shallow experimental trough. The upstream end of the trough was divided into two channels of equal size (fig. 2). As a fish progressed upstream through the experimental trough, it was presented with a choice between the two channels. Differences in water

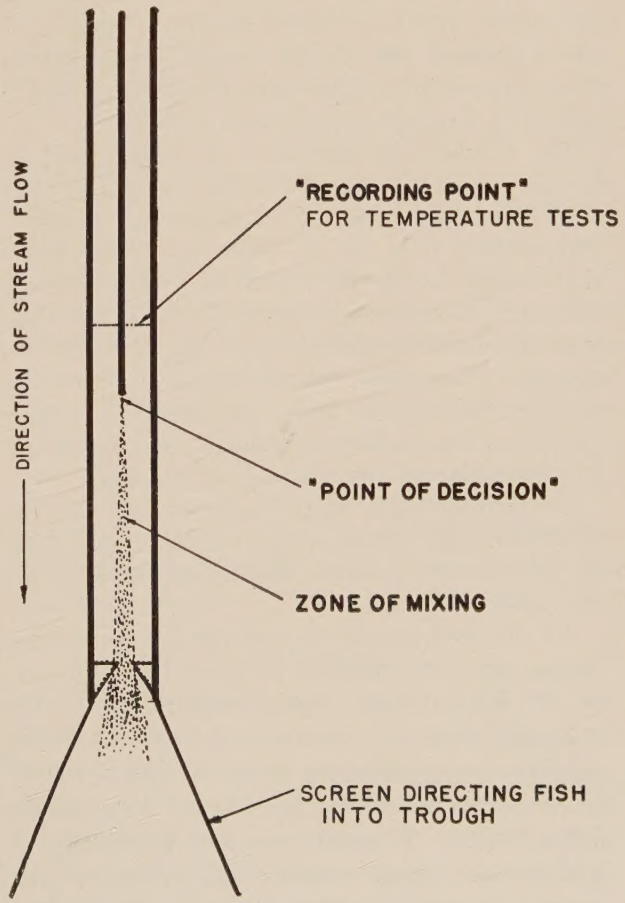

FIGURE 2.—Diagram of experimental trough. Dimensions: 18 ft. long, 21 in. wide, and 10 in. deep.

temperature, in pH, and in dissolved gases between the two channels were created experimentally. The influence of these differences in the physical and chemical characteristics of water upon the orientation of the migrating fish was measured by the number of fish choosing each channel.

The experimental trough was 21 inches wide, 10 inches deep, and 18 feet long. It was open at both ends so that when it was alined with the direction of stream flow and partially submerged, the water flowed freely through it. The two channels in the upstream end of the trough were 10 feet long and 10 inches wide. A 10-inch channel width was chosen because it was approximately equal to the length of the fish and would allow enough room for normal swimming movements and turning. The experimental trough could be raised or lowered in the water in order to create any desired depth of flow regardless of the natural fluctuation in the water level of the stream. The flow of water through the trough was maintained at a depth of 6 to 8 inches, while the velocity of water through the trough varied, depending on stream conditions, from a minimum of 1 foot a second to a maximum of 2 feet a second.

The trough was stained a dull mahogany to provide a dark background for the fish so that their behavior would be as natural as possible. Exploratory tests the previous year had shown that a light background made the fish extremely nervous and excitable when they were in the shallow water and confinement of the experimental trough. The trough was also placed in the stream several weeks before tests were begun to reduce the possibility of odors, or other factors that might be unfamiliar or objectionable to the fish.

To prevent light inequalities between the two channels resulting from shadows, the experimental trough was shaded from direct sunlight by a canvas canopy (fig. 3).

At the downstream end of the trough a wire-screen gate was installed to control the entrance of the fish into the experimental trough. The necessity for such a device became apparent during preliminary exploratory tests in which the entrance of the fish was unrestricted. When several fish entered at the same time, they frequently exhibited a schooling tendency and all followed the choice of the leader. Their behavior was such that it seemed probable that only one decision was

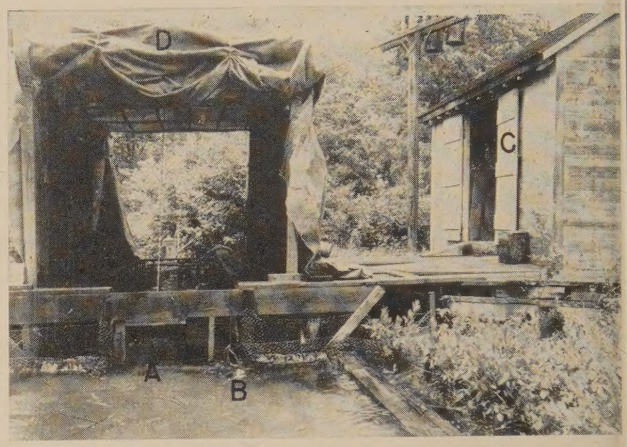

FIGURE 3.—General view of experimental station, Herring River, Bournedale, Mass., 1950.

A. Entrance for upstream migrants.
B. Bypass exit for downstream migrants.
C. Laboratory for chemical determinations.
D. Light-control arrangement.

actually made for the entire school. There were instances of schools splitting, with all those on the left side entering the left channel, and all those on the right side entering the right channel, suggesting that perhaps in these cases spatial relations alone were involved. There were many variations in such group behavior and they were difficult to interpret in a quantitative way. To avoid the problem completely, an entrance gate was designed. Through this gate (figs. 4 and 5) the fish were allowed to enter, one at a time, and only after the previous one had made its decision and was completely out of the trough.

The entrance gate also served to center the fish so that as it entered the experimental trough it was subjected to a mixture of the waters of both channels. Thus, the fish started in the center of a strong transverse gradient (fig. 2) and almost any lateral movement resulted in its being subjected to water of a different quality.

PROCEDURE

As the fish progressed upstream in the trough to the point where it had to choose between the two channels (the "point of decision" in fig. 2), it usually moved from one side of the trough to the other, alternately approaching each channel until it finally entered one. In those tests in which both channels were completely unobstructed the choice was recorded when the fish had completed

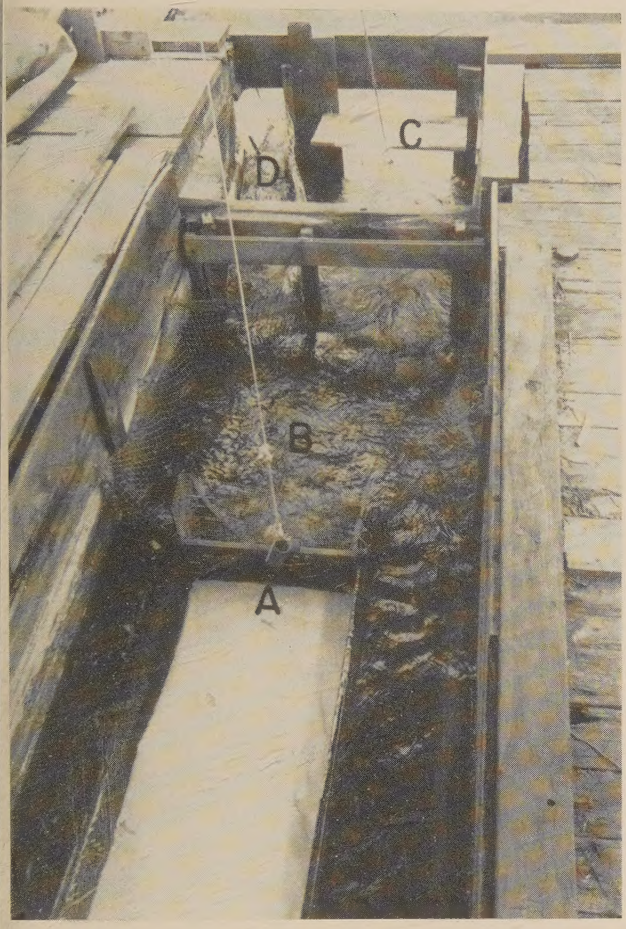

FIGURE. 4.—Entrance to experimental trough.

A. Entrance gate (closed).
B. Retaining pool.
C. Retaining-pool gate (open).
D. Bypass for downstream migrants.

(The white cloth on the bottom of the trough was for photographic purposes and was not present during the tests.)

its passage through the channel and was entirely clear of the trough. This system of recording decisions permitted the fish to change its choice of channels at any stage of its progress by turning back and entering the other channel.

During the experiments in which the water was being modified by heating, the reluctance of the fish to pass through the heating apparatus in the upstream ends of the channels, resulted in considerable delay. To save time a "recording point" (fig. 2) was chosen below the heating apparatus. When this arbitrary point which was 20 inches (approximately twice the length of the fish) from the entrance to the channel was

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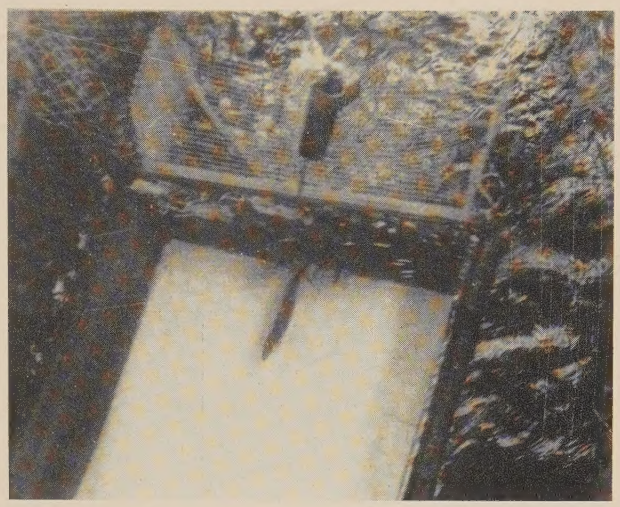

FIGURE 5.—Entrance gate. The fish were allowed to enter, one at a time, through a screen gate (shown open).
(The white cloth was not present during the tests.)

reached, the fish was considered to have made its decision and the result was recorded. When once the fish had passed the recording point if its forward progress was too slow, it was urged to continue on out of the trough by taps on the trough with a stick immediately behind the fish. When the fish was completely out of the trough, the entrance gate was raised again to allow another to enter.

Before each series of tests, any necessary adjustments of experimental conditions were made and water samples and temperature measurements were taken. The fish were then allowed to enter the trough one at a time. It usually was found convenient to run approximately 25 to 30 individual tests in succession before the measurements were taken again. The average time for such a series of tests was about 40 minutes, although it fluctuated considerably depending upon the behavior of the fish.

CONTROLS

Every effort was made to keep conditions, e.g., light, depth of water, rate of flow, turbulence, as uniform as possible in both channels so that any directional response would be due solely to the factor being tested. Whenever major adjustments in the experimental conditions had been made, before tests with modified water were begun, a series of control tests was run to ensure

that such uniform conditions prevailed. The results of these tests are summarized in table 1.

TABLE 1.—*Daily totals of control tests made to ensure that uniform conditions existed in both channels of the experimental trough, 1949*

Date	Number of fish entering—	
	Left channel	Right channel
April 30	91	89
May 1	49	39
2	54	48
3	68	73
7	97	91
8	58	49
11	19	15
12	20	22
14	71	54
15	81	83
16	49	47
19	25	29
22	59	49
23	47	58
24	24	24
30	29	30
Total	841	800
Percent	51.3	48.7

To minimize the possibility of some unrecognized factor influencing the choice of the fish, control and test channels were alternated between each series of tests. Such alternation resulted in any "nonalternating" influence being cancelled out when the figures were totaled. An example of the pattern of controls and tests is given in table 2.

TABLE 2.—*Example of the pattern of controls and tests, May 15, 1949*

[Tests listed in chronological order]

Left channel		Right channel	
Water characteristic [1]	Number of fish	Water characteristic [1]	Number of fish
Control	18	Control	17
CO_2	11	Control	31
Control	26	CO_2	19
Control	25	Control	27
Control	35	CO_2	12
CO_2	11	Control	34
Control	16	Control	16
Control	33	CO_2	17
CO_2	9	Control	26
Control	22	Control	23
CO_2	8	Control	31
Control	31	CO_2	14

[1] Control, water unmodified; CO_2, gaseous CO_2 added.

During tests involving temperature differences of greater than 1 degree centigrade, it was necessary to have a greater number of heaters in one channel than in the other. To be certain that the response shown was the result of temperature differences rather than differences in hydraulic conditions created by the unequal distribution of heating apparatus, a series of control tests was run with the heaters in place but with the power turned off. The results of the control tests which were interspersed with the actual temperature tests are shown in table 3. They indicate that the presence of the nonoperating heaters had little or no effect upon the choice of channels made by the fish.

TABLE 3.—*Control tests during temperature experiments, 1950*

[Immersion heaters in place but power turned off]

Date and time	Number of fish entering—		Number of immersion water heaters in—	
	Left channel	Right channel	Left channel	Right channel
May 13, 3:45 p. m.	16	17	5	5
14, 6:25 p. m.	27	25	0	10
15, 8:00 a. m.	9	8	0	11
20, 10:00 a. m.	12	12	0	11
24, 2:30 p. m.	13	14	0	11
24, 3:30 p. m.	14	13	0	11
25, 4:00 p. m.	26	27	0	11
26, 9:15 a. m.	15	12	0	11
26, 11:30 a. m.	12	15	0	11
27, 10:30 a. m.	21	30	0	8
27, 11:55 a. m.	9	10	0	8
27, 1:30 p. m.	11	15	0	8
27, 4:00 p. m.	8	7	0	8
27, 5:00 p. m.	27	34	0	8
28, 12:40 p. m.	13	12	0	8
28, 2:00 p. m.	13	11	0	8
28, 5:30 p. m.	13	12	3	8
June 3, 8:15 a. m.	7	5	0	11
6, 10:30 a. m.	4	4	0	11
7, 11:15 a. m.	13	15	0	11
Total	283	298		
Percentage	49	51		

WATER MODIFICATION

Temperature

The modification of the water temperature was accomplished by the use of industrial electrical immersion water heaters. These heaters (32 a., 7.5 kw., 230 v.) were of the tubular type and shaped in a simple loop so as to fit easily into the channels of the experimental trough (fig. 6). Each of the 11 heaters was connected separately to the main circuit and could be turned on or off at will without interfering with the operation of any of the other heaters. The arrangement was simple and flexible and made a graded control of temperature possible.

Gaseous Content

The gaseous content of the water was modified by the introduction of specific gases. These gases (O_2, N_2, and CO_2) were bubbled into the water at the upstream end of the trough directly in front

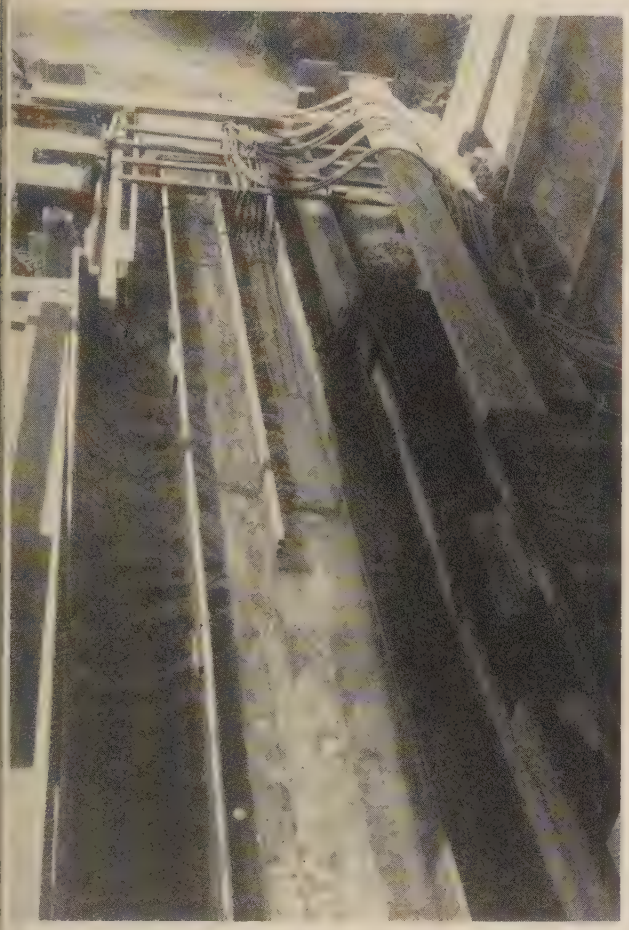

FIGURE 6.—Upstream end of experimental trough during temperature tests. All immersion water heaters are in place for maximum temperature difference.
(Shade on left was raised to allow light for photographic purposes. During the experiments no shadows were present.)

FIGURE 7.—Device for modifying gaseous content of water. The device contained two separate batteries of aerators so that the two channels could be modified independently at the same time.

of the channel or channels in which the water was to be modified.

The device used to accomplish this (fig. 7) consisted of two batteries of porous-stone aerators of the type commonly used in small aquariums. Each battery of aerators produced a band of very fine bubbles. The incorporation of two separate batteries in the same device made it possible to modify independently the water of both channels at the same time.

Nongaseous Chemicals

The nongaseous chemicals used to modify water in experiments were first dissolved in a carboy of water from the stream. They were then introduced at a controlled rate into the upstream end of one of the channels through a colorless plastic tube positioned horizontally an inch above the floor of the trough at right angles to the direction of stream flow. Small holes were bored in the plastic tube at short intervals to allow an even distribution of the carboy liquid throughout the channel.

MEASUREMENTS

Water Samples

Water samples were collected in wide-mouthed 100-milliliter bottles at the downstream end of each channel. Sample bottles were stoppered while still under water to avoid any gaseous exchange with the air. The samples were collected simultaneously in both channels and were immediately brought into the field laboratory where the chemical determinations were begun at once.

Titrations

Titrations were done with a Beckman *p*H meter. The water-sample bottles were calibrated with the solid stoppers on so that the exact amount of water in each sample was known without further measurement. The titrations were performed in the sample bottles to avoid any opportunity for the modification of the gaseous content of the water due to exposure to air in pouring.

Hydrogen-ion Concentration

Measurements of hydrogen-ion concentrations were made to within 0.03 *p*H unit with a Beckman *p*H meter. A Hellige pocket color comparator was used for rapid *p*H measurements (to within 0.1 *p*H unit) during adjustment of valves while setting up experimental conditions and during a number of the earlier exploratory experiments.

Alkalinity and HCO_3

In the range of *p*H in which the experiments were made (*p*H 7 to *p*H 6) the alkalinity was assumed to equal the concentration of HCO_3. Methyl-orange alkalinity was measured (American Public Health Association 1946) by titrating the sample with H_2SO_4 to an end point of *p*H 4.4.

Carbon Dioxide

The free, or uncombined, CO_2 content of the water was measured in two ways. Some of the measurements were made directly by titration of the sample with NaOH (American Public Health Association 1946) to an end point of *p*H 8.2. Other determinations of free CO_2 were made indirectly by measuring alkalinity (methyl orange) and *p*H and then determining CO_2 by the graphic method of Moore (1939). The measurements were made to within 0.1 p. p. m. CO_2. Those measurements made directly by titrating with NaOH were slightly lower than the measurements made indirectly by the graphic method. Therefore, in comparing the water of the two channels only one method was used for each pair of measurements. The range of conditions under which the measurements were made is indicated by figure 8 which shows CO_2 measurements made during the experiments.

During the series of tests which examined the orientative influence of CO_2, water was modified by the introduction of gaseous CO_2. Addition of gaseous CO_2 to the almost unbuffered water of the stream produced several effects. It increased the concentration of free CO_2 and it decreased the *p*H. It also raised the partial pressure, or tension, of CO_2 in the water. Examples of data from individual tests (table 4) illustrate the first two of these effects. It will be noted that the concentration of HCO_3 was largely unaffected. In the range of *p*H in which the experiments were made (*p*H 7 to *p*H 6), carbonates were not present.

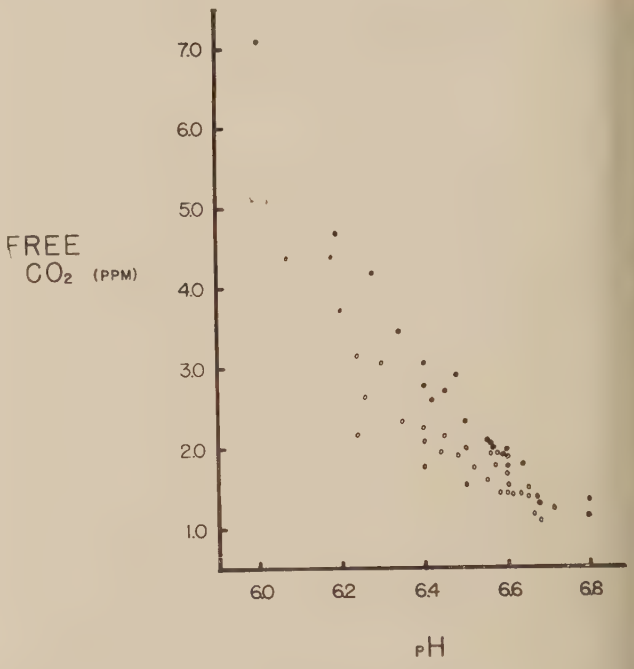

FIGURE 8.—Free CO_2 measurements, May 1950. Only measurements of samples of unmodified stream water and water modified by the addition of gaseous CO_2 are included. The samples were taken under a wide variety of stream and weather conditions.

Water was modified by addition of $K_2H(PO_4)$ during the tests of the orientative influence of *p*H. Examples of data from individual tests are given in table 4. In these tests the changes in *p*H were of approximately the same magnitude as the changes in *p*H in the tests in which CO_2 was added (although $K_2H(PO_4)$ raised the *p*H while CO_2 lowered it). The addition of $K_2H(PO_4)$, however, had much less effect upon the concentration of free CO_2.

During this investigation, measurements of CO_2 were restricted to the convenient and widely accepted methods available for measuring the amount of free CO_2. The importance of measuring dissolved gases in terms of partial pressures

TABLE 4.—*Examples of chemical measurements made during individual tests, June 11, 1950*

[Stream temperatures, 19° to 19.4° C.]

Channel	Water characteristic [1]	Hydrogen-ion concentration	Alkalinity or HCO_3	Carbon dioxide
			P. p. m. Ca CO_3	*P. p. m.*
eft	CO_2	6.40	4.04	3.05
ight	Control	6.57	3.98	2.06
Difference		.17	.06	.99
eft	Control	6.57	3.88	1.95
ight	CO_2	6.18	3.76	4.68
Difference		.39	.12	2.73
eft	Control	6.52		[2] 1.70
ight	$K_2H(PO_4)$	6.97		[2] 1.62
Difference		.45		.08
eft	$K_2H(PO_4)$	6.94		[2] 1.71
ight	Control	6.57		[2] 1.78
Difference		.37		.07

[1] CO_2, gaseous CO_2 added; control, water unmodified; $K_2H(PO_4)$, $K_2H(PO_4)$ added.
[2] Samples titrated with NaOH.

when considering their physiological effects upon organisms is recognized. The ability of a gas to diffuse through a membrane depends upon the tension of the gas in solution. Therefore, the tension of the gas is critical where, as in respiration, an actual gaseous exchange is made. However, very little is known of the sensory mechanism by which fish detect differences of CO_2; nor is it known whether CO_2 must actually permeate a membrane to affect the sensory organs. Under the circumstances of these experiments, where both channels receive water from the same source under identical conditions, the CO_2 tension would be directly proportional to the amount of free CO_2 present. Therefore, the relative amounts of CO_2 in the two channels may be used as indexes of the relative CO_2 tensions.

Oxygen

The amount of dissolved oxygen was determined by the standard Winkler method (American Public Health Association 1946) after preliminary orientation tests (Ellis, Westfall, and Ellis 1948) for the presence of interfering substances proved to be negative.

Temperature

Temperatures were measured to 0.1° C. by the use of a mercury thermometer held horizontally in the water with its long axis in the direction of the current. The measurements were taken at the downstream end in each channel with the center of the thermometer at a point 2 inches from the bottom of the trough (the level at which the fish usually swam) and 2 inches from the wall which divided the trough into two channels.

Velocity

The velocity of the water flowing through the trough was measured by means of an impeller-type current meter. Measurements were accurate to within 0.2 feet per second, and represent the average velocity of the water over a 90-second period of time. The measurements were taken at the downstream end of each channel at a point halfway between the channel walls.

ABERRATIONS IN EXPERIMENTAL CONTROL

Throughout the experiments, measurements of physical and chemical water characteristics such as temperature, velocity, *p*H, and amounts of dissolved gases were much more precise than the experimental control of these characteristics. Hydraulic conditions above the head of the experimental trough created a periodic eddying (every 5 to 15 seconds) which resulted in a fluctuation in the rate of flow alternately in each channel. During tests in which water characteristics were being modified, eddying caused a periodic fluctuation in the degree of modification. For example, during tests in which the water was modified by heating, eddying resulted in a temperature fluctuation of approximately 0.5° C. in the channel being modified.

Temperature measurements to within 0.1° C. were made almost instantaneously, and the extent of the temperature fluctuation was easily measured by a comparison of maximum and minimum temperature readings. However, measurements of other water characteristics such as velocity, *p*H, and amounts of dissolved gases were average measurements. Velocity measurements (read in terms of propeller revolutions per unit time) represented an average velocity for a 90-second period of time. The manner in which the water samples were taken for measurements of *p*H and amounts of dissolved gases tended to collect a mixture of the water flowing through a channel over a period of time greater than the time for a complete cycle of eddy fluctuation and so these measurements also represent measurements of average conditions.

Such average measurements gave no clear indication of the degree of fluctuation.

Some of the other experimental conditions also could not be controlled completely. The depth of the water in the trough, maintained at 6 to 8 inches at the downstream end of the two channels, varied from 4 inches to 10 inches at the ends of the trough when the trough deviated from a horizontal position. The downstream end of the trough had a tendency to settle as a result of the clogging of the screen entrance gate by floating organic debris. Variations of this sort affected the channels equally, however, and probably are of little significance.

During the experiments in which water was heated electrically there frequently was a vertical variation in the temperature of the water in the modified channel due to inadequate mixing of the heated water. This was particularly true when only a few heaters were in operation. At such times, the variation was as much as 0.4° C. from the warmer water near the bottom of the channel to the cooler water near the surface. The temperature measurements, made 2 inches from the bottom of the channel (the level at which the fish usually swam), were always of the maximum temperature.

In interpreting the data collected during these experiments, such variations in experimental conditions must be taken into consideration, particularly when thresholds are concerned. The thresholds for the responses of the fish may actually be lower than those indicated by the data.

EXPERIMENTS

ORIENTATIVE INFLUENCE OF TEMPERATURE

Experiments were conducted in which the migrating fish were presented with a choice between waters of two different temperatures. The responses of the fish (table 5) indicated a preference for the warmer water.

The stream temperature during these experiments ranged from 11.1° to 22.3° C. The temperature differences between channels, created by heating the water of one channel, were varied from 0.4° to 3.0° C. The threshold of the response appeared to be at a temperature difference of approximately 0.5° C.

Periodic eddying which caused a fluctuation in the water temperature of the channel being modified (see Aberrations in Experimental Control, p. 385) was probably responsible for the apparently intermediate nature of the response to temperature differences of 0.5° to 1.0° C. The temperature difference values given in tables 5 and 6 are maximum values. The minimum values were approximately 0.5° C. less. For example, during tests at the recorded temperature difference of 0.7° C., for at least part of the time, the temperature difference was approximately 0.2° C.

Therefore, only at recorded temperature differences above 1.0° C. was the threshold difference of 0.5° C. exceeded continually throughout the entire test.

TABLE 5.—*Response to temperature differences as shown in experiments of May 7 to June 8, 1950*

[Stream temperatures, 11.1° to 22.3° C.]

Water temperature difference between channels [1] (Centigrade)	Number of decisions	Entered channel with—	
		Warmer water	Cooler water
		Percent	*Percent*
0.4°	98	[2] 49	51
0.5°	109	57	43
0.6°	51	61	39
0.7°	180	63	37
0.8°	427	60	40
0.9°	471	61	39
1.0°	76	63	37
Total	1,314	[3] [4] 61	39
1.1°	22	77	23
1.2°	98	80	20
1.3°	136	76	24
1.4°	100	76	24
1.5°	142	77	23
1.7°	98	79	21
1.8°	107	80	20
1.9°	27	78	22
2.0°	83	80	20
Total	813	[3] 78	22
2.2°	213	73	27
2.3°	132	73	27
2.4°	108	83	17
2.5°	28	75	25
2.7°	24	79	21
3.0°	12	75	25
Total	517	[3] 76	24

[1] Temperature differences are maximum values. Minimum temperature differences were approximately 0.5° C. less.
[2] No response.
[3] Response.
[4] See notes on eddying phenomenon, p. 385.

Taking the eddying into account, the intermediate nature of the response to temperature differences from 0.5° to 1.0° C. should probably be discounted and considered as due to imperfect experimental conditions. The data would then be interpreted as describing a uniform ungraded response to temperature differences greater than the threshold.

RELATION OF TEMPERATURE RESPONSE TO TEMPERATURE LEVEL

Tabulation of experimental data according to stream temperature levels (table 6) revealed a general tendency for the response to temperature differences between 0.5° and 1.0° C. to decrease as the temperature level of the stream increased. When the temperature differences between channels were greater than 1.0° C., the temperature level of the stream had no discernible influence upon the response of the fish.

TABLE 6.—*Relation of temperature response to temperature level*

[Retabulation of data from table 5. Stream temperature levels include +0.9° C. (e. g., 11° C. includes temperature levels to 11.9° C.)]

Stream temperature level	Number of decisions	Entered channel with—	
		Warmer water	Cooler water
		Percent	*Percent*
Group A: [1]			
11° C.	139	65	35
12° C.	178	65	35
13° C.	185	65	35
14° C.	274	60	40
15° C.	116	59	41
16° C.	124	55	45
17° C.	66	55	45
18° C.	85	54	46
19° C.	147	53	47
Group B: [2]			
11° C.	35	80	20
12° C.	43	79	21
14° C.	238	77	23
15° C.	217	80	20
16° C.	159	75	25
17° C.	290	76	24
18° C.	198	77	23
20° C.	123	82	18
22° C.	27	78	22

[1] Temperature difference between channels, 0.5° to 1.0° C.
[2] Temperature difference between channels, 1.1° to 3.0° C.

Taking into account once again the eddying condition (see p. 385), the data indicate that the responses of the fish were affected by the temperature level only when temperature differences of threshold magnitudes were concerned. The evidence suggests a possible relation between this phenomenon and the type of threshold phenomena described by Weber's law. Weber (1846) believed the threshold of difference to be proportional to the intensity of stimulus. Although the ratio of these two factors has since been shown to be variable, a tendency for the threshold of difference to increase with an increase in intensity of stimulus has been observed. The experiments at Bournedale, planned with other purposes in mind, did not produce the type of data necessary to examine this particular aspect of the response to temperature differences. However, it seems very probable that the decrease in the response of the fish (shown in group A, table 6) was due to an increase in the threshold of the response to temperature differences as the temperature level of the stream increased.

ORIENTATIVE INFLUENCE OF CO_2

The migrating fish were presented with a choice of waters having different amounts of free, or uncombined, CO_2. The difference in free CO_2 between the waters of the two channels was established by the direct addition of gaseous CO_2 to the water of one channel while the other remained unmodified. During some of the tests this procedure was varied by the addition of the gaseous CO_2 to both channels but at different rates. Throughout the tests the fish indicated a definite preference for the water with the lower free CO_2 content (table 7).

TABLE 7.—*Responses to differences in CO_2 as shown in experiments, May 1–30, 1949, and May 7–June 9, 1950*

Free CO_2 difference between channels	Number of decisions	Entered channel with—	
		Lower CO_2	Higher CO_2
		Percent	*Percent*
>4.0 p. p. m.	1,120	73	27
1.4 p. p. m.	128	77	23
0.6 p. p. m.	663	71	29
0.3 p. p. m.	216	69	31
0.2 p. p. m.	157	59	41

NOTE.—Unmodified stream water varied from 0.7 p. p. m. free CO_2 to 2.9 p. p. m. free CO_2 and pH 6.9 to pH 6.4. Stream temperatures 11.1° to 22.3° C. CO_2 differences listed include differences ±0.1 p. p. m. of listed differences except 0.3 which includes only +0.1 p. p. m.

Whether the fish in the CO_2 experiments were responding to differences in free CO_2 or to associated differences in HCO_3^- is not actually known. The data (table 7) indicate that if the response was to differences in the amount of free CO_2, the threshold of the response lies below differences of 0.3 p. p. m. If the response of the fish was to differences in HCO_3^-, then the threshold of the response must be much lower. During most of the tests in which the differences in free CO_2 were less than 1.0 p. p. m., the differences in HCO_3^- were not even measurable by the method of measurement used (i. e., they were less than 0.1 p. p. m. HCO_3^- as $CaCO_3$). It seems more probable that the response of the fish was a response to free CO_2.

The experiments do not indicate whether the response of the fish (assuming that the response was to free CO_2) was to differences in the amount

of free CO_2 or to differences in CO_2 tension. The difference in CO_2 tension associated with a difference of 0.3 p. p. m. free CO_2 under the conditions of these experiments would be approximately 0.1 mm. Hg.

The response of the fish to differences in CO_2 (whether it was to the amount of free CO_2, to the CO_2 tension, or to associated HCO_3) was similar to the response of the fish to temperature differences in that it appeared to be a uniform response to all differences above the threshold difference.

RELATIVE ORIENTATIVE INFLUENCE OF CO_2 AND TEMPERATURE

As the evidence was acquired indicating that differences in temperature and differences in CO_2 could influence the orientation of the migrating fish, the need for some information on the relative influence of the two factors became increasingly obvious. Under the controlled conditions of the experiments, where all factors other than the one used for testing were maintained equal in both channels, the fish might show as great a response to a relatively minor influence as they would to an important or dominant factor. To examine the relative orientative influence of CO_2 and temperature, two groups of experiments were undertaken. In one set of experiments the directional influences of the two factors were arranged so as to be in conflict. The differences in CO_2 favored the choice of one channel, while the differences in temperature favored the selection of the other. In a second group of experiments the differences both in CO_2 and in temperature favored the selection of the same channel.

The data (table 8) collected indicate that the relative importance of the two orienting factors depends upon their quantitative relationships. By altering the relative amounts of heat and of CO_2 added to the water, it was possible to demonstrate circumstances under which either factor could balance or even dominate the other when the factors were in opposition. The data also suggest that when the two factors are not in opposition they may actually augment each other and together provoke a response in a greater number of fish than either factor could produce alone.

ORIENTATIVE INFLUENCE OF pH

In the preceding experiments involving the addition of gaseous CO_2 to the water, the differences in the amount of free CO_2 between the two channels were always accompanied by differences in *p*H (see table 4). The question arises as to whether the response shown by the migrating fish is to the differences in CO_2 or to the accompanying differences in *p*H.

An attempt was made to answer this question experimentally with the migrating fish. It was necessary to use a substance which would, when added to the water, modify the *p*H of the water to the same degree that it was modified during the CO_2 experiments (see table 9) without, at the same time, materially affecting the amount of free CO_2 in the water. It was also necessary that the substance be one to which the fish would not respond by means such as taste or smell. To avoid the difficulties of determining whether the response of a fish was to the taste or to the smell of a chemical, or whether its response was to *p*H differences created by that chemical, it was necessary to select a substance to which the fish did not respond at all.

In one of a series of exploratory tests (table 10) NaOH was used to modify the water. There was no response to a difference in *p*H of 0.1 (compare with response to *p*H difference 0.1 created by the addition of gaseous CO_2, table 9). However, it will be noted that when the difference in *p*H was greater than 1.0 *p*H unit, the fish favored the

TABLE 8.—*Relative orientative influence of CO_2 and temperature as shown in tests made June 3–11, 1950*

Relation of factors	Water temperature difference between channels	Free CO_2 difference between channels	Number of decisions	Entered channel with—			
				Warmer water and higher CO_2	Cooler water and lower CO_2	Warmer water and lower CO_2	Cooler water and higher CO_2
	° C.	P. p. m.		Percent	Percent	Percent	Percent
Opposing	0.5 to 0.6	>7.0	99	24	76		
	1.8 to 2.1	0.5 to 2.0	129	62	38		
	1.8 to 2.4	2.4 to 7.0	169	48	52		
Augmenting	2.0 to 2.4	0.5 to 2.0	154			83	17

NOTE.—Stream temperatures, 16.9° to 22.2° C. Unmodified stream water, 0.7 p. p. m. to 2.1 p. p. m. free CO_2; pH 7.0 to pH 6.5.

ABLE 9.—*Experiments with CO_2 tabulated according to differences in pH, May 1949*

pH difference between channels [1]	Number of decisions	Percent entering—	
		Higher CO_2	Lower CO_2
1.00	650	30	70
.0	663	29	71
05	114	28	72
.05	157	41	59

[1] Range, pH 6.0 to pH 6.8.

ABLE 10.—*Experiments with NaOH tabulated according to differences in pH, May 24, 1949*

pH differences between channels	Number of decisions	Percent entering—	
		Control channel [1]	Channel with NaOH added [2]
1.00	267	39	61
.10	104	48	52

[1] Unmodified stream water, pH 6.6 to pH 6.8; low pH; high CO_2 content.
[2] High pH; low CO_2 content.

odified water. Although CO_2 was not measured n this test it seems very probable that the difference in free CO_2 which would be associated with he large difference in *p*H would exceed the hreshold 0.3 p. p. m.

After several acids and bases were tried, an experiment was undertaken using $K_2H(PO_4)$ as the odifying agent. The data collected (table 11) eveal no indication of a response on the part of he fish although differences in *p*H were present. hese differences in *p*H were of the same magnitude as those in many CO_2 tests in which the fish esponded. The accompanying table 12 of free CO_2 measurements made while the tests were in progress shows that during the tests differences of ree CO_2 between channels were very small, generally less than the precision of measurement.

ABLE 11.—*Orientative influence of pH as shown in tests made June 10–12, 1950*

[Differences in pH include differences ±0.1 pH unit]

$K_2H(PO_4)$ added	Unmodified control	Difference in pH	Number of decisions	Entered channel with—	
				High pH	Low pH
pH	*pH*			*Percent*	*Percent*
6.7	6.5	0.2	148	49	51
6.9	6.5	.4	127	51	49
7.1	6.5	.6	141	47	53
7.3	6.5	.8	20	50	50
Total			436	49	51

TABLE 12.—*Measurements of free CO_2 taken during the tests shown in table 11*

[Samples titrated with NaOH]

$K_2H(PO_4)$ added	Unmodified control	Difference in free CO_2	Difference in pH
P. p. m.	*P. p. m.*	*P. p. m.*	
1.94	1.96	0.02	0.2
1.62	1.69	.07	.3
1.71	1.78	.07	.4
1.62	1.70	.08	.4
1.31	1.45	.14	.6

On the basis of the evidence from this experiment, it would seem reasonable to conclude that the response shown by the migrating fish in the previous tests was a response to differences in CO_2 rather than a response to differences in *p*H.

EXPERIMENTS USING NITROGEN AND OXYGEN

Nitrogen

During the tests with CO_2, particularly those tests in which the CO_2 had been added to only one of the two channels, the possibility had to be considered that the physical presence of many bubbles in the modified channel might be influencing the choice of the fish. To eliminate this possibility nitrogen was used as a control. The gaseous nitrogen was bubbled into the water of one of the channels in the same manner and at the same rate as the CO_2 in the previous experiments. The addition of the N_2 produced no measurable difference in the amount of dissolved O_2. The data (table 13) reveal that the fish failed to show any response to the nitrogen or to the presence of the many bubbles produced. The nitrogen was then used as a control in a series of CO_2 tests. The results of these tests show the same response to CO_2 that was shown in previous tests, again indicating that the presence or absence of the bubbles had no influence upon the choice of the fish.

Oxygen

To investigate the orientative influence of O_2, the migrating fish were presented with a choice of waters which contained different amounts of dissolved O_2. The water of one of the channels was modified by the addition of gaseous O_2. The experiment, however, was severely limited by the fact that the water of the stream was already more than 100 percent saturated. The data in table 13 show that the fish did not respond to a relatively small difference in O_2 under these conditions. The

TABLE 13.—*Experiments testing orientative influence of oxygen and nitrogen*

Factor	Number of decisions	Entered control channel	Entered channel with—		
			N_2 added	CO_2 added	O_2 added
		Percent	*Percent*	*Percent*	*Percent*
Nitrogen bubbles	300	50	50		
Nitrogen (control)	477		71	29	
Oxygen [1]	344		50		50

[1] Stream temperature, 15.4° to 19.1° C. O_2 content of unmodified stream water, 10.5 to 10.7 p. p. m. O_2 difference between channels, 1.1 p. p. m.

experiments unfortunately provide no information on the possible effect of differences in O_2 at lower values where differences may be very important.

OTHER FACTORS INFLUENCING ORIENTATION

Although the major experimental efforts of this investigation were concerned with the orientative influence of temperature and dissolved gases, exploratory experiments also examined the influence of other factors.

The influence of water velocity upon the orientation of the migrating fish was explored by subjecting the fish to a choice between waters of different velocities. The difference in velocity between the two channels was created by placing a glass plate across the upstream entrance to one of the channels, restricting the amount of water entering that channel and so reducing the velocity of the water in the downstream end of the channel. The response of the fish (table 14) indicated that water velocity could be a factor in fish orientation.

The influence of water turbulence upon the orientation of the fish was explored in a similar manner. The turbulence in one of the channels was reduced by placing glass plates, several feet in length, in the center of the channel parallel to the channel walls. This produced a flow which was smooth and laminar in appearance. In the other channel, small glass plates were set at an angle to create eddies which produced a visible turbulence. Most of the fish selected the channel with less turbulence (table 15). CO_2 was then added to the channel with less turbulence in order to discover the relative influence of turbulence and CO_2. The data indicate that CO_2 had the greater orientative influence.

TABLE 14.—*Orientative influence of velocity*

Water velocity		Number of decisions	Entered channel with—	
Right channel	Left channel		Higher velocity	Lower velocity
Ft./sec.	*Ft./sec.*		*Percent*	*Percent*
1.5	0.7	26	85	15
0.7	1.0	26	65	35

TABLE 15.—*Orientative influence of turbulence and CO_2*

Influence of—	Number of decisions	Entered channel with—	
		Maximum turbulence	Minimum turbulence
		Percent	*Percent*
Turbulence	26	32	68
Turbulence and CO_2	27	70	[1] 30

[1] CO_2 added, 4 p. p. m.

An exploratory experiment was made which indicated that visual factors may influence fish orientation. The downstream end of one channel was partially blocked (see fig. 9). The fish normally swam within a few inches of the bottom of the trough so that the "obstacle" did not interfere in any physical way with their progress. However, most of the fish entered the channel which was completely unobstructed. To examine the relative influence of this visual factor and temperature, the water of the partially blocked channel was heated 2° C. The data (table 16) show that under these conditions temperature was the dominant orienting factor.

These tests were crude experiments of an exploratory nature. There undoubtedly were some velocity differences involved in the turbulence tests. The partial block at the downstream end of one of the channels in the tests involving the visual factor probably created slight differences

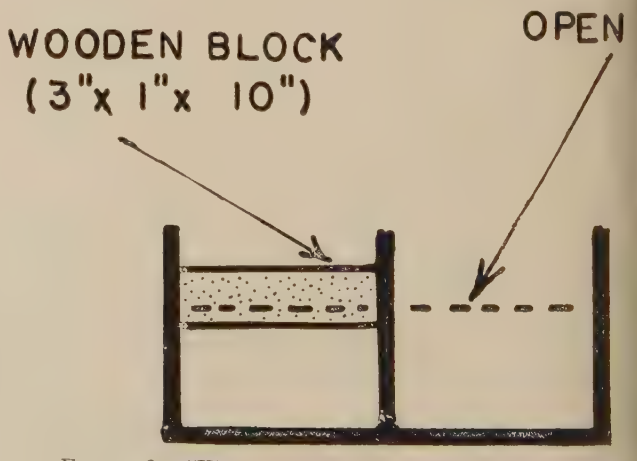

FIGURE 9.—"Visual" factor (exploratory tests).

TABLE 16.—*Orientative influence of the visual factor*

Influence of—	Number of decisions	Entered channel that was—	
		Open	Obstructed
		Percent	*Percent*
sual factor	89	65	35
mperature and visual factor.	93	40	[1] 60

[1] Heat added, 2° C.

hydraulic conditions between the two channels. he experiments were done with relatively small umbers of fish and the degree of the response hould not be interpreted too literally. However, ne experiments are presented here because they o indicate that characteristics of flow, such as elocity and turbulence, can have a directional nfluence upon migrating fish. They also indiate that, under some circumstances at least, isual factors are capable of influencing fish rientation.

THE 3 : 1 RATIO OF THE RESPONSE

The explanation for the persistence of the approximately 3 : 1 ratio in the response of the fish to emperature differences and to CO_2 differences is ot readily apparent. The absence of a response nuch closer to a 100 percent response under such ontrolled conditions would seem to indicate that nly a proportion of the fish were influenced by he orienting factor. If, for example, half of the ish were influenced by the testing factor and the ther half entered the channels at random, the esulting ratio would be 3 : 1.

A possible sexual variation in the response of he fish was considered. A trap was placed at the ead of each channel and after a series of CO_2 ests had been run, the fish in each trap were xamined for sex. This procedure was later repeated with a series of temperature tests. The lata (table 17) indicate that the sex of the fish as no effect upon its response to differences in CO_2 and temperature.

The possibility of individual variation in the ensitivity of the fish to temperature differences nd to CO_2 differences was examined by gradually ncreasing the differences between the two chanels. Had there been significant individual variation in sensitivity, the response would have become greater as the difference between channels gradually exceeded the thresholds of more and more fish. This, however, did not occur. The response remained approximately 3 : 1 even at the maximum attainable differences (>7.00 p. p. m. free CO_2 and 3.0° C.).

TABLE 17.—*Influence of sex on the response to CO_2 and temperature*

Factor and sex	Number of decisions	Percent that entered channel with—			
		CO_2 content—		Temperature—	
		Higher	Lower	Higher	Lower
CO_2:					
Male	54	26	74		
Female	70	27	73		
Temperature:					
Male	24			79	21
Female	38			76	24

The possibility was also considered that some individuals might be completely insensible to the differences in temperature and CO_2 which were being used in the experiments. An experiment was set up in which fish that had previously been tested were again subjected to the same choice. A trap was placed at the head of each channel and a series of CO_2 tests were made. The trapped fish were then brought back to the entrance of the experimental trough and the CO_2 tests repeated. The data (table 18) show that the response of the fish that had previously entered the channel with the higher CO_2 was approximately 3 : 1 in favor of the channel with the lower CO_2, and those fish which had previously entered the channel with the lower CO_2 also exhibited a 3 : 1 response in favor of the channel with the lower CO_2.

Such evidence strongly suggests that the 3 : 1 ratio is not due to the failure of particular individuals or particular groups of individuals to respond to the orienting factor. It seems more probable that the explanation lies in the behavior patterns inherent in all the fish. If, for example, every fish responded to an orienting factor only half the time and acted at random the other half, the result would also be a 3 : 1 ratio. Further

TABLE 18.—*Retesting the response of fish to CO_2*

Fish from channel with—	Number of decisions	Entered channel with—	
		Higher CO_2	Lower CO_2
		Percent	*Percent*
Lower CO_2	111	27	73
Higher CO_2	54	30	70

experiments may be necessary to throw some light on the nature of the ratio and to learn whether the phenomenon has any significance beyond the restricted circumstances of this experimental method.

DISCUSSION

When the results of the preceding experiments are compared with the findings of other investigators several interesting possibilities are suggested. One possibility is that the response of the fish to temperature differences might be a family characteristic. The two species of fish, *Pomolobus pseudoharengus* (Wilson) and *Pomolobus aestivalis* (Mitchill), which at Bournedale showed a consistent preference for warmer water, are members of the family Clupeidae. Shelford and Powers (1915) found that herring, *Clupea pallasi*, fry preferred warmer water. The observations of Roule (1933) indicated that migrating shad, *Paralosa nilotica rhodanensis* and *Alosa alosa*, which also belong to the family Clupeidae, selected water of higher temperature.

The threshold of the response to temperature differences shown by the two species of fish at Bournedale (0.5° C.) agrees very closely with that reported by Shelford and Powers (1915) for herring fry. This threshold may seem high compared to the minimum effective thermal stimulus range for certain fresh-water fishes (differences of 0.03° to 0.07° C.) reported by Bull (1936). However, it must be remembered that this temperature difference represents the minimum temperature difference which will provoke an unconditioned orientative response in the fish. The minimum temperature difference which can be perceived by the fish is probably much less.

Powers and Hickman (1928) presented evidence to show that rivers draining lakes usually had lower CO_2 tensions than other rivers (average difference 0.5 mm. Hg). Powers (1939) contended that by means of these differences in CO_2 tension migrating fish could select certain types of streams. The results of the CO_2 experiments at Bournedale would fit well into his argument. The alewife and the glut herring both showed a strong preference for water of lower CO_2 tension (threshold difference 0.1 mm. Hg). These fishes usually spawn in small ponds and shallow lakes and the choice of water of lower CO_2 content would result in the selection of streams leading to lakes or ponds.

The fundamental nature of the response of the fish to differences in CO_2 and to differences in temperature is indicated by the manner in which CO_2 and temperature were able to dominate competing orienting factors in the exploratory tests shown on page 390. The low threshold values for these responses also suggest their probable importance.

The experiments examining the orientative influence of *p*H (p. 388) confirm the conclusion of Powers (1930) that *p*H was largely ineffective as a factor influencing the behavior of aquatic animals. Whether the response of the fish in the experiments at Bournedale was to differences in free CO_2 or to the associated differences in HCO_3 was not actually established although the threshold values involved suggest that the response was to free CO_2. If the response was to the free CO_2 the influence of CO_2 differences is limited to waters with a *p*H of less than 8.4. This fact might be used to advantage in an experiment to determine to which of the two factors the fish are responding.

Although the main efforts of this investigation were directed toward examining the orientative influence of CO_2 and temperature upon the migrating fish, this was not meant to imply that these are the only major influences which might be concerned in other situations. The influence of differences in dissolved O_2 may be of great importance when lower O_2 values are concerned, which was not the case at Bournedale. Under special conditions flow characteristics such as velocity and turbulence may play an important part in directing the fish. The role of olfactory memory needs to be further explored. The influence of factors affecting the orientation of the fish indirectly (e. g., by controlling the depth of swimming) must be considered. It was largely to stress the fact that many factors may be concerned in fish orientation that the exploratory tests involving velocity, turbulence, and visual factors were included in this report.

Perhaps one of the most important considerations to which the foregoing experiments call attention is that not only are there many factors which may have a directional influence upon the migrating fish but also that they must all be considered together. The experiments examining

he relative influence of CO_2 and temperature emonstrated conditions under which the response o temperature differences could dominate the re-ponse to CO_2 differences when the factors were n opposition. The reverse situation was also emonstrated. The experiments further revealed ircumstances under which the two factors were qual and the influence of the one balanced the nfluence of the other. Had an observer at these xperiments been considering only temperature, or example, he would have seen the fish choose he warmer water in one group of tests and the older water in another. During the third group f tests he would have concluded that the fish ere indifferent to temperature. It is quite pos-ible that many apparently contradictory observa-ions may be explained in this way, e.g., the bservations of Ward (1920), Chamberlain (1907), and Foerster (1929), regarding the in-luence of temperature on sockeye salmon.

One of the considerations that had to be taken nto account during the experiments at Bourne-ale was that the fish might be reacting to a hange in water conditions. This possibility be-ame evident in one of the exploratory tests ex-mining the influence of light intensities. One hannel of the experimental trough was shaded nd the other was left exposed to full sunlight. When the undivided lower portion of the experi-ental trough was shaded, the fish chose the haded channel. When the lower part of the rough was exposed to sunlight, the fish chose the unlit channel. Thus the fish showed no prefer-nce for either the sunlit or the shaded channel. They simply avoided any change in light onditions.

During experiments in which water was modi-ied by the introduction of gaseous CO_2 the fish voided the modified water. Although the fish ntered the trough in a mixture of water from oth channels (fig. 2), and before entering they ad been subjected to a mixture of both waters in he upstream end of the retaining pool (fig. 4), he possibility that the reaction of the fish was ne to change in chemical conditions still had to e considered. However, in one experiment which was made at Bournedale, the CO_2 content f the water of one channel was reduced by the ddition of NaOH. In that experiment (see p. 388) the fish showed a preference for the modified water. It, therefore, seems improbable that the response of the fish in the other CO_2 experiments was a response to change in chemical conditions.

Powers and Clark (1943), discussing certain gradient-tank experiments with brook trout, *Salvelinus f. fontinalis*, and rainbow trout, *Salmo gairdneri iridus*, presented evidence indicating that the reactions of the trout to CO_2 in these experiments might be characterized as reaction to change. They made the observation that "The immediate response to carbon dioxide tension of the water depends to a large extent upon the carbon dioxide tension to which the fish is adjusted." The period of adjustment in their experiments was only 10 to 15 minutes.

If this observation were true for migrating fish then CO_2 would probably have little directive influence. The fish adjusted to the CO_2 tension of the sea would be restrained from entering fresh water with a different CO_2 tension. At a junction between two streams the fish would tend to select the stream with the larger volume in an effort to remain in the CO_2 tension nearest to the one to which it had become adjusted.

A possible explanation is suggested by an earlier statement of Powers (1939):

> The ova and sperm heads contain a protein (protamine) containing large percentages of arginine. It requires a vast protein metabolism to obtain the necessary arginine. Protein metabolism and especially fasting—both necessary for the liberation of arginine from the muscular tissue of the salmon—tends to produce acidosis of the blood, *i. e.*, lower the alkali reserve of the blood. This is common knowledge. A salmon with a low alkali reserve blood would find low carbon dioxide tension water more advantageous.

The special physiological state of the migrating fish might prevent it from becoming adjusted to its environment.

As experimental evidence is acquired indicating physical and chemical differences may have a directional influence upon migrating fish, the method by which the fish is oriented to these differences becomes an important consideration, particularly when one is trying to relate artificial experimental conditions to situations found in nature.

There are two methods by which fish might become oriented in a gradient. The fish might make a simultaneous comparison of intensities of stimu-

lation by means of symmetrically placed receptors and turn toward (or away from) the maximum stimulation. If this was the method of orientation, the orientative influence of gradients would be limited to those gradients great enough so that the differences between points a few inches apart (the distance between paired receptors) are above the threshold of sensory perception of fish. Gradients as high as this do actually exist in nature but usually only as a narrow zone between two bodies of water which are just beginning to mix.

A second method by which a fish might orient in a gradient is similar to the "trial" method of orientation characterized by Jennings (1906) as "selection from among the conditions produced by various movements." He points out that in this type of behavior, "Each stimulus causes as a rule not merely a single definite action that may be called a reflex, but a series of "trial" movements, of the most diverse character, and including at times practically all the movements of which the animal is capable." This type of orientation Fraenkel and Gunn (1940) have labeled "klinotaxis," and defined as "a directed orientation made possible by means of regular deviations and involving comparison of intensities at successive points in time," and they pointed out examples of such behavior in many invertebrates. In this method of orientation the fish, subjecting itself to varied conditions by its active movements, would select the most favorable condition or direction. The method involves both movement and comparison of intensities of stimulation that are successive in time.

The behavior of the fish as they selected a channel in the experimental trough at Bournedale strongly suggested that this latter method of orientation is the one used. As the fish entered the trough they usually swam from one side to the other, approaching first one channel and then the other. When once the fish had left the narrow zone in which the water was mixing (fig. 2) it was no longer subjected to a gradient. Its sensory receptors were all subjected to the same intensity of stimulation and, therefore, the current was the only orientative influence directing the movement of the fish upstream, unless memory was involved. Yet the fish repeatedly swam from one side of the trough to the other and frequently even after entering one channel, they turned back and entered the other.

Orientation by means of a comparison of intensities that are successive in time would make it possible for fish to become oriented in much smaller gradients than would be necessary if orientation was by a simultaneous comparison of intensities. The minimum gradient in which a fish could orient would depend on the speed of the fish and the time interval of its sensory memory.

The experiments at Bournedale have demonstrated that one group of migrating anadromous fishes will orient with reference to differences in certain physical and chemical water characteristics created artificially. It is logical to suppose that the fish will also be oriented by similar differences occurring along their migration routes in nature.

SUMMARY

The purpose of this investigation was to examine experimentally the influence of certain physical and chemical water characteristics upon the orientation of one type of migrating anadromous fish. The migrating fish were presented with a choice between two channels that carried water with different characteristics. The orientative influence of the water properties in question was measured by the number of fish selecting each channel. The reactions of more than 8,000 fish of the genus *Pomolobus*—alewife, *P. pseudoharengus* (Wilson), and glut herring, *P. aestivalis* (Mitchill)—were tested as the fish migrated upstream through the Herring River at Bournedale, Mass., toward their spawning area, in the springs of 1949 and 1950.

The fish were not removed from the stream or handled in any way. Each was tested individually and tested only once (the few exceptions are noted). The findings of this investigation were:

1. Presented with a choice of waters having different temperatures, 77 percent of the fish entered the channel with the warmer water when the temperature difference continuously exceeded 0.5° C. The temperature differences examined ranged from 0.4° to 3.0° C. Water temperatures during experiments varied from 11.1° to 22.3° C.

2. The response of the fish to temperature differences near the threshold difference decreased as the temperature level of the water increased.

3. Presented with a choice of waters having different amounts of free CO_2, 72 percent of the fish entered the channel with water of a lower

ee CO_2 content when the free CO_2 difference ceeded 0.3 p. p. m. (0.1 mm. of Hg in terms CO_2 tension). The differences in free CO_2 exnined ranged from 0.2 p. p. m. CO_2 to greater an 4.0 p. p. m. The amount of free CO_2 in the ater during these experiments varied from 0.8 p. m. to 7.1 p. p. m.

4. The sex of the fish appeared to have no inience on its response to differences in CO_2 connt or in temperature.

5. Exploratory experiments indicated that visal factors and such factors as velocity and rbulence can influence orientation.

6. The fish did not respond to a difference of 1 p. m. m. O_2 created during experiments. The mount of O_2 in the water during the experiments nged from 10.5 p. p. m. to 10.7 p. p. m. and ater temperatures ranged from 15.4° to 19.1° C.

7. The fish were indifferent to *p*H differences large as 0.8 *p*H unit when associated differences free CO_2 were less than the threshold 0.3 p. p. m. he *p*H of the water varied from 6.5 to 7.3 during ese experiments.

8. The relative orientative influence of CO_2 d temperature, when the two factors were in position, was shown to depend upon their relave differences of magnitude. A difference in mperature of approximately 2° C. dominated opposing difference in free CO_2 of 2.0 p. p. m. difference of CO_2 slightly in excess of 2.4 p. p. m. alanced the opposite effect of a 2° C. temperare difference. A difference of >7.0 p. p. m. CO_2 ominated over a temperature difference of 0.6° C.

9. The behavior of the fish during the experients indicated that the orientation was accomlished by a method of "trial" involving both ovement of the fish and a comparison of insities of stimulations which were successive time.

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